Space and time use in syntopic populations of *Akodon azarae* and *Calomys venustus* (Rodentia, Muridae)

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Abstract

Spatial use and activity times were studied in syntopic populations of *Akodon azarae* and *Calomys venustus* in agroecosystems of southern Cordoba Province (Argentina). Space use was determined by recording co-occurrence of both species at the same trap station whereas activity times were obtained by means of traps fitted with timers that started at the animal capture. Data were analysed during reproductive and non-reproductive periods. Spatial co-occurrence of *A. azarae* with *C. venustus* was recorded in both periods. A separation between the species under study was observed in the niche temporal axis. *A. azarae* showed continuous activity with variational peaks depending on the reproductive and non-reproductive periods whereas *C. venustus* showed activity during crepuscular and night hours in both periods. Consequently, these differences in the times of resource use are likely to be the main mechanism for syntopic co-existence of *A. azarae* and *C. venustus*.

Introduction

In small-rodent communities inhabiting agroecosystems of southern Cordoba Province (Argentina), *Akodon azarae* and *Calomys venustus* are frequently captured in the same type of habitat (Kravetz and Polop 1983; Polop et al. 1985; Polop and Sabattini 1993). This seems to indicate that both populations are likely to have access to the same type of resources. However, an axiom of multidimensional niche theory (Hutchinson 1957) holds that each species will have a limited specificity, within a range, for each dimension. Thus, coexistence of *A. azarae* and *C. venustus* could be explained only to the extent in which each species uses the niche dimensions in a different way. *A. azarae* and *C. venustus* populations are characterized by seasonal density changes, annual turnover, iteroparous reproduction and cohort-specific reproductive tactics (Crespo 1966; Pearson 1967; Dalby 1975; Zuleta 1989; Polop 1996).

In studies on rodent communities, food not always seems to be limitative; for this reason it has been suggested that habitat differences would become the main mechanism to prevent interference competition (Schoener 1974; Meserve 1981). It is also assumed that coexistence between sympatric populations is given not only by segregation at the level of the niche spatial dimension but also by a separation at the level of the temporal dimension. Differences in the latter dimension seem to be the mechanism that best explains how to reduce interference competition (Carothers and Jaksic 1984; Canova 1993).

On the basis that the hypothesis of multidimensional niche (Hutchinson 1957) will explain coexistence between *A. azarae* and *C. venustus*, the aim of this study was to determine spatial use and activity time of these two species in agroecosystem habitats.

Material and methods

The study was carried out in Chucul (64° 20′ 09″ West, 32° 21′ 06″ South) Rio Cuarto Department, Cordoba Province, Argentina. Phytogeographically this region corresponds to the "Provincia del Espinal" "Distrito del Algarrobo" (CABRERA 1953). This is a plain at a low elevation (600–900 m) with vegetation dominated by algarrobo (*Prosopis alba, P. nigra*), accompanied by quebracho blanco (*Aspidosperma quebracho blanco*), mistol (*Zizyphus mistol*) and itin (*Portulaca kuntzie*). The vegetation, however, has undergone marked alterations as a result of agriculture and cattle farming. At present, the landscape mainly consists of individual cropfields, surrounded by wire fences with borders dominated by weedy species. In the area, the railway banks are an environment where some rodent populations reach high densities. Plant community is characterised by pasture interspersed with bushes. Despite the influence of nearby crop fields, it bears some resemblance with indigenous vegetation. This environment was selected for sampling.

Rodents were caught from April 1990 to February 1995 in traps arranged in a grid of 6×10 traps (50 m×90 m) with an interestation interval of 10 m per one Sherman live trap, placed in each station, baited with a mixture of peanut butter and cow fat. Monthly censuses were taken in periods of 5 successive days. Traps were checked daily in the morning.

Co-occurrence of the two species was recorded in the same trap station during the same sampling period to measure spatial overlapping. Co-occurrence values were taken as indicators of the fact that co-occurrent species used the same space. In this way the space was circumscribed to the micro-habitat of each trap station influential area. Only resident animals were taken into account for co-occurrence computation. Residents were defined as animals caught more than once in the same or different sampling periods.

Between 1992 and 1994, traps were fitted with a timer started by trap closing to determine activity times of animals in the field. The time elapsed between capture and trap checking was recorded. In this way each animal capture time could be estimated. Activity time was taken as a measure of animal activity periods in the grid area. A total of 511 capture times were registered, 362 of *A. azarae* and 149 of *C. venustus*.

Trapped animals were weighed, measured and marked with a numerical code in the ears. Sex and reproductive state (males: scrotal or abdominal testicles, females: perforated or imperforated vagina, nipples visible or not) were also recorded.

Data were analysed by considering separately the non-reproductive period (May to August) and the reproductive period (September to April) since it was found that spatial use and activity times are likely to vary according to the seasons or to the annual cycle of the population (O'FARREL 1974; MUÑOZ-PEDREROS et al. 1990; FRANK and HESKE 1992; Muñoz-Pedreros 1992).

Population size was estimated by computing the minimum number of animals known alive (MNKA) (KREBS 1966).

Co-occurrence between *A. azarae* and *C. venustus* was analysed by means of COLE (1949) association index: $C = a \cdot d - b \cdot c/(a + b) \cdot (b + c)$ if $a \cdot d \geq b \cdot c$; or $C = a \cdot d - b \cdot c/(a + b) \cdot (a + c)$ if $b \cdot c > a \cdot d$ and $d \geq a$; or $C = a \cdot d - b \cdot c/(b + d) \cdot (c + d)$ if $b \cdot c > a \cdot d$ and $a > d$; and co-occurrence percentage $(a \cdot 100/a + e)$; where a = number of trapping stations where both species were captured, b = number of trapping stations where only the first species was captured, c = number of trapping stations where only the second species was captured, d = number of trapping stations where none of the species was captured and e = number of trapping stations where the less frequent species was captured.

The relationship between population sizes of the species and between population sizes and monthly co-occurrence was established by means of Lineal Regression Analysis, in which co-occurrence was considered as the dependent variable and population size of each species as the independent variable.

Temporal variation between *A. azarae* and *C. venustus* was determined by the Chi-square test of independence.

Results and discussion

From April 1990 throughout February 1995, 510 *A. azarae* (1,374 captures), 300 *C. venustus* (529 captures) were trapped during 14,880 trap-nights. Figure 1 shows the variations in abundance mean values after 5 sampling years for *A. azarae* and *C. venustus*. *A. azarae*

was the most abundant species for the major part of the two periods in each sampling year, the abundance values being at their minimum in spring and at their maximum in autumn-winter. The displacement in population peaks between the species under study is noticeable. The abundance, throughout the 57 months of census, of *A. azarae* did not vary significantly in relation to the abundance of *C. venustus* ($R^2 = 0.031$; D. F.: 55). This fact suggests that interference competition is not involved. As studies by Geuse and Bauchau (1985) show for *Clethrionomys glareolus* and *Apodemus sylvaticus*, we can also assume that the absence of relation between presence or abundance of one species and the other is evidence of a low interspecific competition.
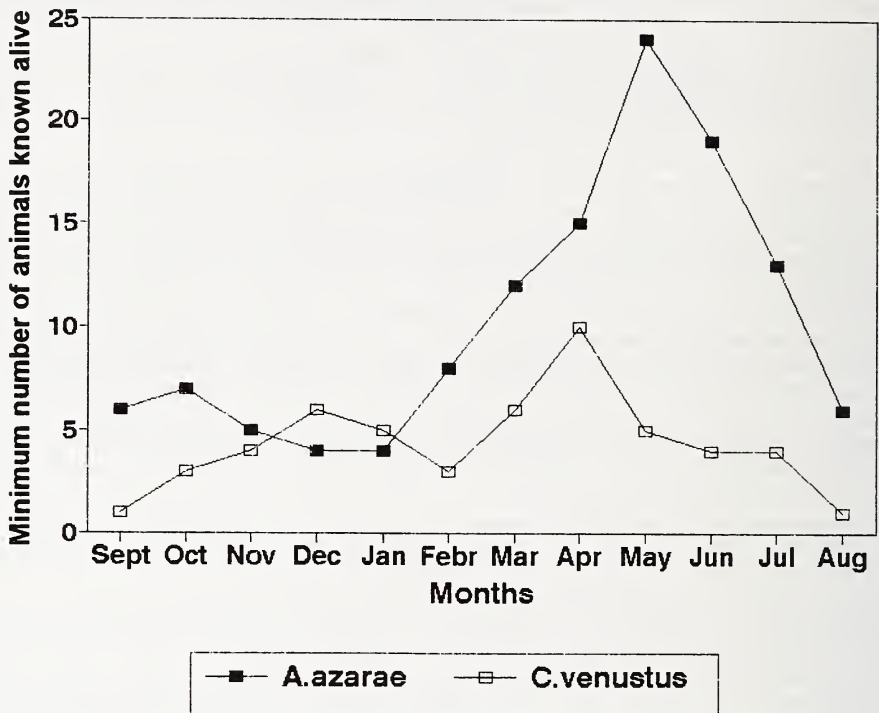

Fig. 1. Average values of monthly abundance variation (MNKA) for *Akodon azarae* and *Calomys venustus* in railway banks habitats (Río Cuarto Department, Córdoba, Argentina, 1990–1995).

Results about spatial dimension did not reveal a separation between *A. azarae* and *C. venustus* since neither species showed differences in spatial use, keeping co-occurrence in both reproductive and non-reproductive periods. The values of the Cole association index and co-occurrence percentages for non-reproductive and reproductive periods are shown in table 1. Differences in spatial use were detected and a higher co-occurrence was observed in the non-reproductive period. The high co-occurrence values (values >20%) between *A. azarae* and *C. venustus* were associated to low and positive values of the Cole association index, and related to a random spatial use. Individuals from both species co-occurred in a trap station with members of the opposite as well as the same sex. Co-occurrent animals included both young and adult individuals. Given the possibility of higher co-occurrence frequency in the non-reproductive period due to more abundance, determination of differences in co-occurrence degree between sampling periods became of paramount importance. In this way it was possible to verify whether differences in co-

occurrence represented differences in social spacing or just density differences. When determining the ratio of co-occurrence proportion over population sizes the values were: 0.12 (D.F.: 48) and 0.25 (D.F.: 48) for *A. azarae* and *C. venustus*, respectively. These results show that the two species are not likely to be conditioned by a social factor in space use, i.e., individuals from both species would not feel compelled to co-occur because of abundance. Instead, they would co-occur due to absence of territoriality among them. BROWN and ORIANS (1970) observed that absence of interspecific territoriality is economically beneficial in habitats where high restriction in exploitation models prevents adequate divergence in resource use. This is the railway banks case, i.e. heterogeneous habitats compared to the rest of agroecosystem habitats, but they do not offer a large variety of microhabitats which allow a differential resource exploitation.

Table 1. Cole association index and co-occurrence percentage by annual period in *A. azarae* and *C. venustus* of resident populations in railway banks (Córdoba, Argentina).

	Non-reproductive period		Reproductive period	
	A. azarae n = 368	*C. venustus* n = 84	*A. azarae* n = 356	*C. venustus* n = 168
Co-ocurrence %	35.7		20.2	
Cole index	0.05		0.02	

n = number of individuals on which Cole index and co-occurrence percentages were estimated.

An important separation between *A. azarae* and *C. venustus* was observed in the niche temporal axis for reproductive and non-reproductive periods. Thus, *A. azarae* showed 24-hour activity with peaks varying according to the population annual cycle, whereas activity of *C. venustus* concentrated in crepuscular and night hours (Figs. 2 and 3). A similar behaviour to that of *A. azarae* was previously observed in other species of *Akodon* (Muñoz-Pedreros et al. 1990). In the reproductive period *A. azarae* activity decreased during daytime shifting to evening and night. In the same period *C. venustus* increased its activity times between evening and dawn with peaks between 9.00 p.m. and 3.00 a.m. (Fig. 2). In the reproductive period the differences among activity times in both species were statistically significant (Chi-square = 66.08; $P = 9.10 \times 10^{-12}$; D.F.: 7). During the non-reproductive period, differences in activity times between *A. azarae* and *C. venustus* were statistically significant with a Chi-square value of 65.77 ($P = 1.05 \times 10^{-7}$; D.F.: 7). *A. azarae* was active mainly during daytime and crepuscular hours, increasing its activity between 6.00 a.m and 9.00 p.m., whereas *C. venustus* was particularly active between 6.00 p.m. and midnight (Fig. 3). Although activity time differences were significant in both periods, higher temporal segregation took place in the non-reproductive period in which *A. azarae* showed a more diurnal behaviour. This could be accounted for by a more pronounced co-occurrence in the spatial axis during this period. However, a comparison between co-occurrence values in capture stations and population sizes of each species showed they were not conditioned by a social factor in space use. Nonetheless, differential time use in the same space could be a hiding factor. Differences in activity times due to the need of reducing the possibility of encounters, have been reported for other rodent species (LAMBIN and BAUCHAU 1989). Evidence about *A. azarae* and *C. venustus* diet (BILENCA et al. 1992; POLOP 1996) shows partial overlapping. Consequently, a higher differentiation in the activity times may be the main mechanism for the use of the same space and food. This conclusion agrees with that of CAROTHERS and JAKSIC (1984) who hold that differences in activity times are generated by interference competence, as a way to make coexistence
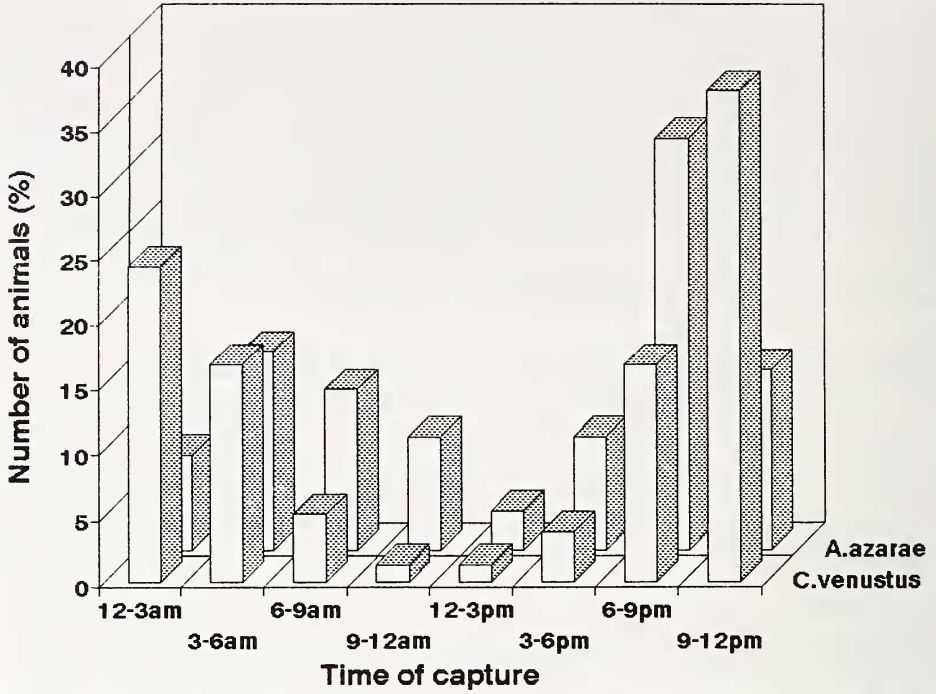
Fig. 2. Temporal distribution of *Akodon azarae* and *Calomys venustus* during the reproductive period in railway banks (Río Cuarto Department, Córdoba, Argentina).
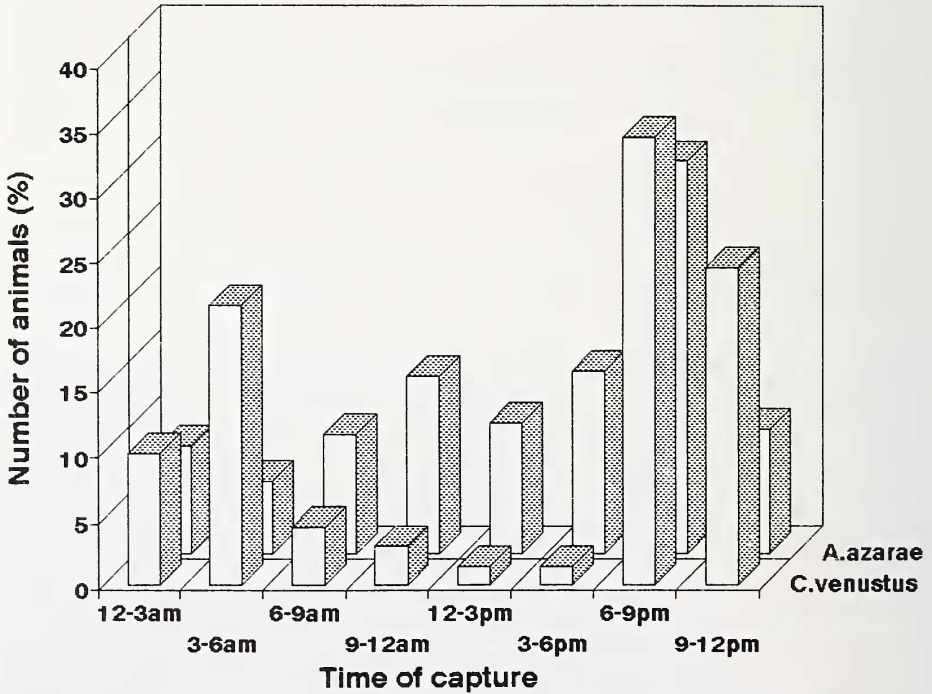

Fig. 3. Temporal distribution of *Akodon azarae* and *Calomys venustus* during the non-reproductive period in railway banks (Río Cuarto Department, Córdoba, Argentina)

feasible among species presenting agonistic interaction. Anyway, it is commonly held that only experimental data reveal interference competence (SCHOENER 1983). Also, segregation in niche dimensions in sympatric populations may reflect either the effects of past or present competition or the ecological preferences of allopatric ancestors that coexist today (CONELL 1980). Although there are no data available about the evolutionary past of these species, we know that they come from regions and probably from habitats completely different from the sampled ones (REIG 1986) and that they are morphologically and physiologically well adapted to habitats like the one under study (KRAVETZ and POLOP 1983; ZULETA 1989). Sympatric coexistence among these species might therefore be explained in the same way as that suggested by CANOVA (1993) for *Apodemus sylvaticus* and *Clethrionomys glareolus* because *A. azarae* and *C. venustus* originally lived in different habitats. Segregation in the present niche dimensions might, therefore, reflect the habitat, food preferences and activity times imposed by their original habitats.

Acknowledgements

Zusammenfassung

Nutzung von Raum und Zeit bei syntopischen Populationen von Akodon azarae und Calomys venustus (Rodentia, Muridae).

Gegenstand der Studie waren die Nutzung des Raums und die aktiven Zeiten bei syntopischen Populationen von *Akodon azarae* und *Calomys venustus* in Agro-Ökosystemen im Süden der Provincia de Córdoba (Argentina). Die Raumnutzung wurde mittels des Registers des gleichzeitigen Auftretens der beiden Arten in derselben Fallenanlage bestimmt, während die aktiven Zeiträume mittels mit Chronometern ausgestatteten Fallen erhalten wurden, die sich im Moment der Gefangennahme aktivierten. Die Daten wurden je nach reproduktiver und nicht-reproduktiver Periode analysiert. Dabei wurde das gleichzeitige räumliche Auftreten von *A. azarae* und *C. venustus* sowohl während der reproduktiven als auch während der nicht-reproduktiven Periode festgestellt. Auf der zeitlichen Achse des Ökosystems konnte jedoch eine Trennung der beiden untersuchten Arten beobachtet werden. *A. azarae* zeigte eine kontinuierliche Aktivität mit je nach der reproduktiven oder der nicht-reproduktiven Periode variierenden Spitzenwerten, während *C. venustus* in beiden Perioden vor allem in Stunden der Abenddämmerung und der Nacht aktiv war. Diese Unterschiede in den Nutzungszeiten der Ressourcen konstituieren daher den Mechanismus der Koexistenz bei Syntopie von *A. azarae* und *C. venustus.*

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